Polish J. of Environ. Stud. Vol. 19, No. 6 (2010), 1229-1237

*Original Research*

# How Decomposition of Organic Matter from Two Soil Layers Along an Altitudinal Climatic Gradient is Affected by Temperature and Moisture

**Beata Klimek*, Maria Niklińska**

Institute of Environmental Sciences, Jagiellonian University,
Gronostajowa 7, 30-387 Kraków, Poland

*Received: 11 February 2010*
*Accepted: 29 April 2010*

**Abstract**

The aim of our study was to assess the influence of temperature and soil moisture on the respiration rate of two soil organic layers (Olf, Ofh), taken from forested sites located at four altitudes (600, 800, 1,000, 1,200 m a.s.l.) on different mountains (Beskidy Mts, Poland). In a factorial laboratory experiment, combinations of temperature and moisture levels were used during short-term incubation of soils. While soil sensitivity to climatic factors did not differ between the stands from different altitudes, the respiration of the lower organic layer Ofh was more sensitive to temperature changes than respiration of the upper Olf layer.

**Keywords:** respiration, altitudinal gradient, forest organic layer, temperature sensitivity, soil moisture

## Introduction

Temperature and soil moisture directly influence the activity of soil decomposers and are the most important factors affecting the rate of organic matter decomposition [1]. It has been suggested that the sensitivity of decomposition to global warming may be latitude-dependent, with the response to global warming being greater at higher than at lower latitudes. These differences can have meaningful significance because of large amounts of carbon stored in soils of higher latitudes [2-4]. Mountain areas with vertical gradients of temperature and precipitation provide an opportunity to observe climate changes similar to those observed at various latitudes. However, our previous study [5] on the altitudinal transect in the Beskidy Mts indicated that the altitude effect was significant for the organic layer respiration rate but not for $Q_{10}$ values (respiration rate change between two consecutive temperatures).

$CO_2$ efflux from the soil is strongly influenced by soil properties and the quality and quantity of organic substrates [6]. A number of studies have shown that temperature sensitivity of decomposition can vary depending on litter type and decomposition stage, but investigating the temperature sensitivity of different organic matter fractions has proven difficult [7]. One idea is that a more chemically recalcitrant organic matter fraction of deeper soil layers is relatively more sensitive to temperature than the surface organic layer [8-10], and thus is more important in the global carbon balance because it constitutes a larger pool of organic matter. The higher thermal sensitivity of more recalcitrant compounds of old organic matter may be caused by higher activation energy ($E_a$) required to break the chemical bounds [11]. Some studies have shown that the upper soil layer could be more sensitive to temperature changes [12, 13]. Elevated temperature may affect the size of available carbon pool for microorganisms, thereby shifting microbial communities to be more adapted to higher temperatures [14, 15].

It has been shown that soil processes in different ecosystems are primarily a function of soil temperature [2, 9], but moisture level also controls soil respiration [16]. Nevertheless, studies of the effect of interaction between

*e-mail: beata.klimek@uj.edu.pl

Table 1. Mean annual temperature and precipitation on plots on different mountain elevations.

| Elevation (m a.s.l.) | type of ecosystem | mean annual temperature (ºC) | mean annual precipitation (mm) |
|---|---|---|---|
| 600 | lower montane (mixed forest) | 7.2 | 1000 |
| 800 | lower montane (mixed forest) | 5.8 | 1050 |
| 1,000 | lower montane (mixed forest) | 4.8 | 1250 |
| 1,200 | upper montane (coniferous forest) | 3.8 | 1420 |

temperature and moisture on the respiration of soils from altitudinal transects are limited. Knoepp and Swank [17] found the significant effect of temperature and soil moisture on nitrogen mineralization rates in soils from southern Appalachian Mountains. Moreover, Powers [18] suggested that soil moisture limited the nitrogen mineralization of low elevated sites while temperature was the most important factor for soil from high elevation.

Despite an increasing number of studies on the impact of temperature and moisture on soil organic matter decomposition and carbon cycling in terrestrial ecosystems, there are still substantial uncertainties about whether climate change will shift ecosystems from being important carbon sinks to carbon sources [19-21]. The aim of the present experiment was to estimate the effect of different combinations of temperature and moisture on the respiration rates of forest organic matter originating from two soil layers (Olf, Ofh) from stands at four altitudes (600, 800, 1,000, 1,200 m a.s.l.) in the Beskidy Mts. The selected forest soils were markedly different in organic matter layers that may represent two stages of litter decomposition. We hypothesized that the sensitivity of respiration to changes in both climatic parameters (temperature and soil moisture), measured as $Q_{10}$ coefficients, should differ between the soil from different altitudes. We also wanted to check if the lower organic layer with more recalcitrant organic matter fractions is more sensitive to climatic changes than the upper layer.

## Materials and Methods

### Study Plots and Soil Sampling

The study plots were situated along the altitudinal gradient at 600, 800, 1,000, and 1,200 m a.s.l. in southern Poland in the Beskidy Mts, part of the Western Carpathians, in the study conducted in summer 2005. Three mountain peaks at similar latitudes and of similar geological structure were chosen: Polica (1,369 m a.s.l.) and Romanka (1,366 m a.s.l.), both in the Beskid Żywiecki range and Radziejowa (1,262 m a.s.l.) in the Beskid Sądecki range. Together twelve plots were marked out (combinations of mountain and elevation). Since mountain soil temperature and moisture depend highly on the slope and insolation, all plots were selected on north-directed slopes. All the mountains are located on approximately the same E-W parallel and were treated as experimental replicates. The differences in mean annual temperature and precipitation between the lowest and the highest plots of elevation gradient were 3.4ºC and 420 mm, respectively (Table 1).

The plots at the three lowest altitudes are covered by 30-40-year-old spruce forests mixed with beech, alder, and fir; 50-year-old spruce forests predominate on the plots at 1,200 m. The plant species composition of the forests at the lower altitudes has been affected by human activities such as nearby agriculture, pasturing, and collection of litter from the forest floor [22]. The soils at the sampling plots were generally podzol and brown earth.

At each plot, ten samples from two distinguished humus layers (Olf and Ofh) were collected at ten points 10 m apart from each other, horizontally across the slope. The upper layer Olf contains fragments of leaves and needles; organic matter in the lower Ofh layer was completely shredded. Soil organic layers (Olf and Ofh) were characterized by different thicknesses, ranging from 1 to 12 cm, depending on plant cover. Soil samples were immediately sieved (1 cm) to remove stones, roots, and the green parts of plants, thoroughly hand-mixed, and transported to the laboratory.

### Effect of Temperature and Soil Moisture on Respiration Rate

The soil dry weight was determined by drying three subsamples (from each plot and each organic layer) at 105ºC for 24 h. The organic matter content was determined as loss on ignition at 550ºC for 24 h. Water holding capacity (WHC) was measured by the standard gravimetric method with three replicates.

The soil respiration rate was measured in equivalents of 10 g dry weight for the Olf layer and 20 g dry weight for the Ofh layer, because of markedly lower soil organic matter content in Ofh layer. The samples were incubated at 5ºC, 15ºC, and 30ºC, and at three soil moisture levels: 15%, 75%, and 120% WHC in three climatic chambers (precision ±1°C). Sample moisture were kept constant by adjusting weekly with deionised water. Altogether 648 samples were used (combinations of mountain, altitude, OM layer, temperature and soil moisture, with three replicates for each treatment). During one day the respiration rate was measured in 108 samples.

The respiration rate of each sample was measured weekly for three weeks by trapping $CO_2$ in 5 ml 0.2 M NaOH in airtight glass jars. After incubation of the samples in the closed jars for 12-48 h (depending on the incubation temperature and soil moisture), 2 ml $BaCl_2$ were added to the NaOH solution, and the excess of sodium hydroxide was titrated with 0.1 M HCl, in the presence of phenolphthalein as an indicator. Empty jars randomly distributed among the others for each incubation temperature and moisture were used as blanks. Between measurements the jars were left open. The respiration rate for each sample was expressed as mM $CO_2$ per kg organic matter per 24 h. At the end of incubation the organic matter content was determined for each tested soil sample for accurate estimation of the respiration rate of soil organic matter in each sample.

The $Q_{10}$ temperature coefficients were calculated using the mean respiration rates measured at two subsequent incubation temperatures: $Q_{10}L$ for the two lower temperatures (5ºC-15ºC) and $Q_{10}H$ for the two higher temperatures (15ºC-30ºC), at the different soil moisture levels. The $Q_{10}$ coefficients were calculated for samples from each plot, each organic layer, and each moisture treatment, using the average respiration rates ($R_1$ and $R_2$) at the two consecutive temperatures (T1 and $T_2$) [23]:

$$Q_{10} = \left(\frac{R_2}{R_1}\right)^{10/(T_2 - T_1)}$$

## Chemical Analyses

Chemical analyses were performed for soil samples from each plot and organic layer. Soil pH was measured in 2 g subsamples shaken for 1 h in 20 $cm^3$ deionized water or 1M KCl. The concentrations of nutrients (Ca, Mg, Mn, K, Na, C, and N) in soil were also determined. Total Ca, Mg, Mn, K, and Na were measured after wet digestion of 0.5 g subsamples in 10 ml concentrated $HNO_3$. Three blank samples and three replicates of standard certified material (Rye grass, PROMOCHEM, GmbH) were analyzed with each set of samples. Ca, K, and Na were measured by emission flame spectrometry (JENWAY, PFP 7), and Mg and Mn by flame atomic absorption spectrometry (PERKIN-ELMER, AAnalyst 800). Total C (carbon) and N (nitrogen) contents were analyzed with a CHNS analyzer (Elemental Analyzer GmbH, Vario EL III).

## Statistical Analysis

Two-way ANOVA was used to test for differences in the physicochemical parameters between organic matter layers (Olf, Ofh) and elevations (600, 800, 1,000, 1,200 m a.s.l.), and the interactions between them. The measured parameters included OM content, pH in water, and pH in KCl, concentrations of Ca, Mg, Mn, Na, K, and N, and C:N ratios. When differences were found, the means were compared using Tukey's test and the results were considered significant at $p<0.05$. Non-significant interactions ($p>0.05$) were removed from models. To satisfy ANOVA model assumptions, we log-transformed Mn concentrations to normalize the data.

Multifactor ANOVA was applied to test the significance of the effects of elevation, organic layer, incubation temperature, and moisture, and the interactions between them, on the log respiration rate. Multifactor ANOVA was applied to estimate the influence of elevation, organic matter level, temperature ranges, and moisture, and the interactions between them, on the log $Q_{10}$ coefficients. When differences were found, the means were compared using Tukey's test and the results were considered significant at $p<0.05$. Non-significant interactions ($p>0.05$) were removed from models. To satisfy ANOVA model assumptions, we log-transformed respiration rate and $Q_{10}$ values to normalize the data.

Simple regressions were applied to test the relationships between $Q_{10}$ values and C:N ratios under different moisture conditions. When a statistically significant relationship was obtained, regression lines were compared to test the relationships between $Q_{10}$ values and C:N ratios at lower and higher temperature ranges. All statistical analyses employed Statgraphics ver. 5.1.

# Results

## Soil Chemical Properties

The organic matter content differed significantly between both studied organic layers ($p<0.0001$) (Table 2), but the effect of elevation and of the interaction between elevation and organic layer were not significant. Organic matter content was higher in the Olf layer at all altitudes. Elevation exerted a significant effect on pH in water ($p<0.02$) and pH in KCl ($p<0.04$), while the organic layer and the interaction between elevation and organic layer had no significant effect on pH. There were no differences in Ca, Mg, K, and Na concentrations between organic layers or between elevations, and there was no significant effect of the interaction between them. Only elevation significantly affected log(Mn) concentration ($p<0.02$). The organic layer had a significant effect on N concentration ($p<0.007$), but the effect of elevation and the interactive effect were not significant. The C:N ratio varied between organic layers ($p<0.05$) but not between elevations, and the effect of interaction between them was not significant.

## Respiration Rate and $Q_{10}$ Values

The mean respiration rate ranged from 2.68 mmol $CO_2$ $kg^{-1}$ OM 24 $h^{-1}$ (Radziejowa Mt., 1,200 m a.s.l., Ofh layer, 5ºC and 120% WHC) to 74.99 mmol $CO_2$ $kg^{-1}$ OM 24 $h^{-1}$ (Radziejowa Mt., 800 m a.s.l., Olf layer, 30ºC and 75% WHC). Multifactor ANOVA for the log respiration rate showed a significant effect of elevation ($p<0.0001$), organic layer ($p<0.0001$), incubation temperature ($p<0.0001$) and soil moisture during incubation ($p<0.0001$) (Fig. 1A). There were significant interactions between elevation and organic layer ($p<0.0001$), between temperature and organic layer ($p<0.0003$), and between temperature and moisture ($p<0.002$) (Fig. 1B).

Table 2. Main properties of Olf and Ofh forest organic layers along the studied elevation gradient.

| parameter | elevation (m a.s.l.) | organic matter layer | |
|---|---|---|---|
| | | Olf | Ofh |
| organic matter1) | 600 | 54.1±2.2[b] | 27.0±4.6[a] |
| | 800 | 46.7±16.9[b] | 23.7±4.6[a] |
| | 1,000 | 56.2±10.6[b] | 32.2±12.5[a] |
| | 1,200 | 58.4±6.2[b] | 40.0±0.8[a] |
| | | OML*** | |
| pH in water | 600[b] | 4.3±0.3 | 4.1±0.2 |
| | 800[ab] | 4.1±0.0 | 4.0±0.0 |
| | 1,000[ab] | 4.0±0.3 | 3.9±0.2 |
| | 1,200[a] | 3.9±0.1 | 3.7±0.1 |
| | ELEV* | | |
| pH in KCl | 600[a] | 3.3±0.4 | 3.1±0.2 |
| | 800[ab] | 3.1±0.1 | 3.1±0.1 |
| | 1,000[ab] | 3.0±0.3 | 2.9±0.3 |
| | 1,200[b] | 2.8±0.3 | 2.7±0.1 |
| | ELEV* | | |
| Ca[2)] | 600 | 3,877±2,031 | 2,052±1,840 |
| | 800 | 2,378±1,270 | 1,293±999 |
| | 1,000 | 2,136±299 | 1,588±747 |
| | 1,200 | 1,442±763 | 1,661±434 |
| Mg[2)] | 600 | 1,343±198 | 1,460±977 |
| | 800 | 1,028±515 | 1,458±938 |
| | 1,000 | 519±146 | 1,599±1,478 |
| | 1,200 | 1,340±1,024 | 477±86 |
| Mn[2)] | 600[a] | 687±324 | 451±365 |
| | 800[ab] | 530±217 | 382±104 |
| | 1,000[ab] | 304±20 | 252±161 |
| | 1,200[b] | 285±141 | 321±35 |
| | ELEV* | | |
| K[2)] | 600 | 1,353±276 | 1,332±862 |
| | 800 | 967±56 | 1,349±480 |
| | 1,000 | 856±17 | 1,978±1,750 |
| | 1,200 | 1,780±942 | 858±52 |
| Na[2)] | 600 | 41±11 | 39±28 |
| | 800 | 30±25 | 51±26 |
| | 1,000 | 25±24 | 47±31 |
| | 1,200 | 44±22 | 29±9 |

Table 2. Continued.

| parameter | elevation (m a.s.l.) | organic matter layer | |
|---|---|---|---|
| | | Olf | Ofh |
| N[1)] | 600 | 1.60±0.44[b] | 1.12±0.33[a] |
| | 800 | 1.67±0.41[b] | 1.12±0.33[a] |
| | 1,000 | 2.02±0.03[b] | 1.44±0.57[a] |
| | 1,200 | 2.04±0.10[b] | 1.61±0.13[a] |
| | | OML** | |
| C:N | 600 | 19±3[b] | 19±2[a] |
| | 800 | 19±3[b] | 18±3[a] |
| | 1,000 | 22±2[b] | 18±3[a] |
| | 1,200 | 21±2[b] | 19±3[a] |
| | | OML* | |

Values are means±SD (n=3)
[1)] As percent of dw.
[2)] As parts per million dw.
Different subscripts letters denote differing elevation (ELEV) or organic matter layer (OML) effect on particular soil properties. Statistical significances of main effects are shown below each set of means.
* P<0.05
** P<0.01
*** P<0.001

The mean values of the $Q_{10}$ coefficients ranged from 1.28 (Olf layer, 1,000 m a.s.l., incubation temperature range 15-30°C, 120% WHC) to 3.67 (Ofh layer, 1,200 m a.s.l., 5-15°C, 120% WHC). Multifactor ANOVA for the log $Q_{10}$ values showed a significant effect of incubation temperature range (p<0.0001), moisture level (p<0.0002), and organic layer (p<0.0001) (Fig. 2). The elevation had no significant effect (p>0.1) and no significant interaction was found. The calculated mean values of $Q_{10}L$ were significantly higher than the mean values of $Q_{10}H$. This means that acceleration of the decomposition rate was higher in the 5-15°C range than in the 15-30°C range. The mean $Q_{10}$ value for the Ofh organic layer was significantly higher than for Olf. This means that the respiration rate of organic matter from the Ofh layer was more sensitive to temperature changes than that of the Olf layer. For both layers the mean $Q_{10}$ values for 15% moisture were higher than for 75% or 120% WHC.

The relationship between log $Q_{10}$ values and C:N ratios was significant only under moderate moisture conditions 75% WHC (p<0.03) (Fig. 3A). In this case comparison of the regression lines for the relationship between $Q_{10}L$, $Q_{10}H$ and the C:N ratio showed that $Q_{10}L$ was higher than $Q_{10}H$ (Fig. 3B). In these moisture conditions, the calculated model was significant at p<0.001 and the intercepts were different, but there were no differences between slopes.

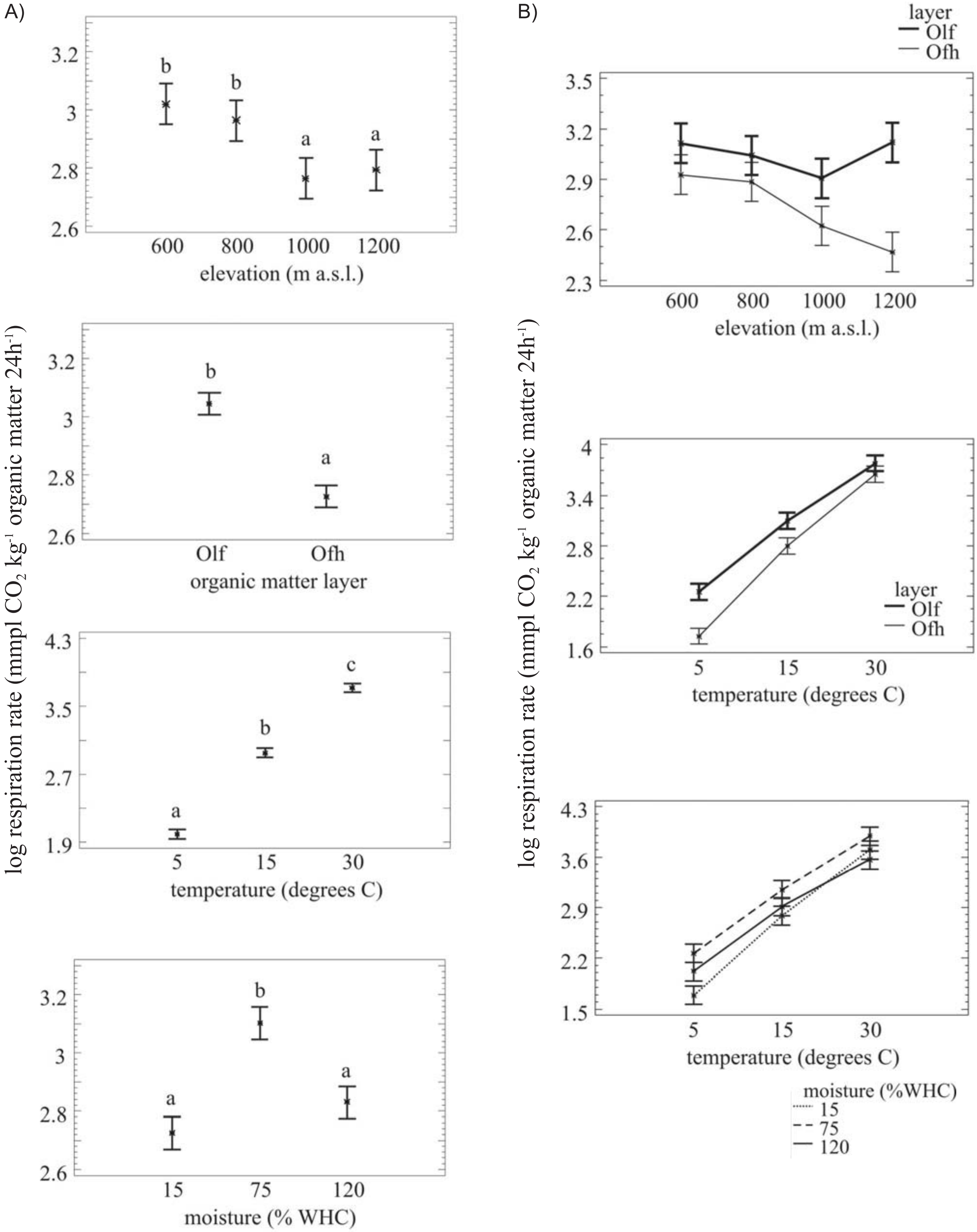


Fig. 1. A) Effect of elevation (n=54), organic matter layer (n=108), incubation temperature (n=72), and incubation moisture (n=72) on log respiration rate. Central points indicate the sample means, and error bars indicate 95% Tukey HSD intervals. Different letters above bars indicate significant differences.

B) Interaction effects on log respiration rate between elevation and organic matter layer, between temperature and organic matter layer, and between temperature and moisture.

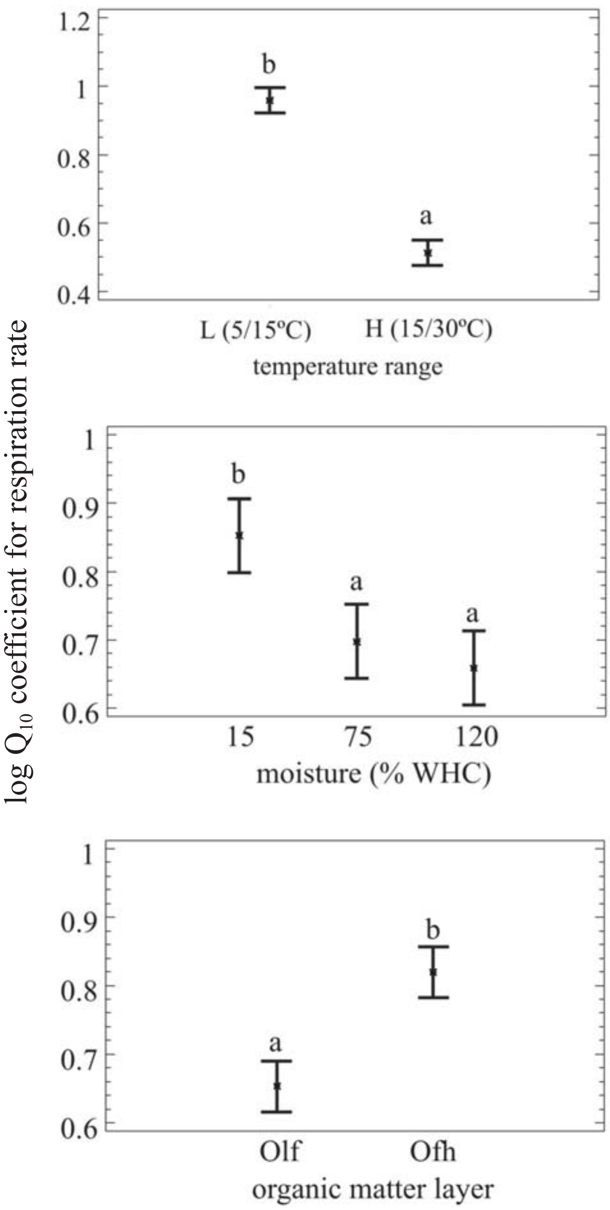


Fig. 2. Effect of temperature range (n=72), moisture (n=48), and organic matter layer (n=72) on log $Q_{10}$ values. Central points indicate the sample means, and error bars indicate 95% Tukey HSD intervals. Different letters above bars indicate significant differences.

## Discussion

### Soil Chemical Properties along the Elevation Gradient and in Organic Matter Layers

Although the plant species at the studied sites differed to some extent, there were no significant differences in the concentrations of nutrients such as Ca, Mg, K, and Na between elevation or between the organic layers. Only Mn concentration and soil pH (measured in water and in KCl) differed significantly between altitudes, but not between the Olf and Ofh layers. The Olf and Ofh layers differed significantly only in the organic matter content and in nitrogen concentration and thus the C:N ratio. Contrary to expectations, we did not find significant differences in organic matter content and C:N ratio along the 600 m elevation gradient, characterized by less than 4ºC degree difference in annual mean temperature. The lack of the significant relationship between altitude and organic matter parameters despite the observed changes in plant composition along the mountain elevation gradient, could be caused by man-made influence on floristic composition at the studied sites. The increase of spruce admixture with elevation may cause differences in the chemistry of soil organic matter, in particular by increasing the recalcitrant litter fraction, as waxes, resins and lignin, and by reducing pH as observed in this study. In fact, similar co-variation is found in a parallel climatic gradient [24]. The C:N ratio differed significantly between organic layers, and was lower in the bottom (Ofh) layer. The decreasing values of C:N ratios down the soil profiles was found also by [25] and [26].

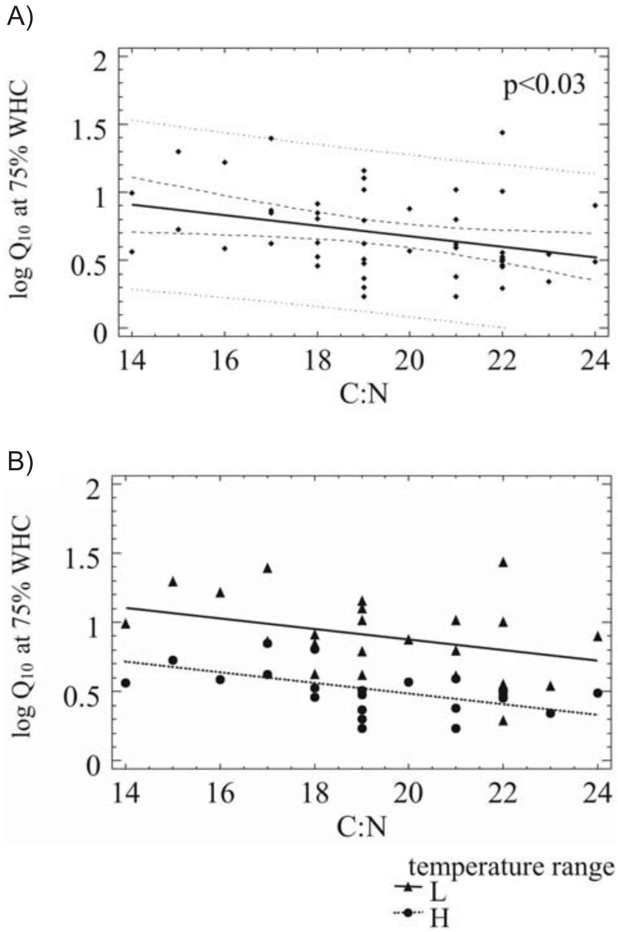


Fig. 3. A) Relationship between log $Q_{10}$ values for respiration rate at 75% WHC and soil C:N ratios (n=38). The model was significant at $p<0.03$.
B) Comparison of regression lines between log $Q_{10}$ values for respiration rate at lower (L) and higher (H) temperature range and C:N ratios at 75% WHC moisture level (n=38). Model was significant at $p<0.0001$; the intercepts of regression lines for $Q_{10}L$ and $Q_{10}H$ at 75%WHC differed statistically and the slopes were equal.

## Soil Respiration Rate

Respiration rate is significantly dependent on temperature; increasing temperature enhanced the respiration rate of samples from all tested elevations and from both tested organic layers. Temperature could affect the soil respiration rate by altering the microbes' metabolism, biomass and/or community structure [27]. In the laboratory analysis of the soils, respiration was significantly dependent on soil moisture. The respiration rates were low at 15% and 120% WHC (dry and very wet conditions) and significantly higher at 75% WHC. Similar effects of temperature and soil moisture on respiration rates have been reported [1, 20, 28]. In fact, in wet and warm conditions (120% WHC and 30ºC) the anaerobic atmosphere might cause the release of methane in addition to carbon dioxide. Methane emission was not measured in this study, but the observed effect of the interaction between temperature and moisture effect on soil respiration rate might have been due to it. Furthermore, we did find that the temperature-moisture interactions significantly affected the soil respiration rate. This means that an increase in soil temperature may enhance microbial activity unless limited by soil moisture conditions. The significant effects of temperature and temperature-moisture interaction on soil activity measured as nitrogen mineralization was shown previously [17].

Additionally, significant interactions in respiration rate were found between elevation and organic layer and between temperature and organic layer. The interaction between temperature and organic layer indicates that higher temperature is needed to decompose more complex chemical compounds in the more decomposed Ofh layer. The respiration rate calculated per unit of organic matter (kg) was significantly lower in the Ofh than in Olf layer. Similar results were obtained by [29]. The lower respiration rate of Ofh than Olf layer indicated that the deeper layer represented the more recalcitrant organic matter fraction. But, it was stressed that old soil C is not always recalcitrant itself [7]. Unfavorable conditions such as physical and chemical protection, drought, flooding, and freezing, may prevent it from decomposition [10]. Also, the lower soil respiration rates in samples from 1,000 and 1,200 m a.s.l. may indicate poorer substrate quality or less favourable climatic conditions. Soil organic matter decomposition is carried on mainly by microorganisms, so low microbial community activity reflect these poorer-C and colder climatic conditions.

The plot of the interaction between elevation and organic layer shows an exceptionally high respiration rate for the upper organic matter layer (Olf) from 1,200 m a.s.l., while the respiration rate for the Ofh layer at the same elevation was very low. We have no clear explanation for this phenomenon. It might be due to high mean nutrient concentrations (Mg, K, Na), but high variability caused the differences between the Olf and Ofh layers at 1,200 m a.s.l. site to be insignificant (Table 2).

## Factors Affecting Soil Thermal Sensitivity ($Q_{10}$)

Apart from the absolute differences in respiration rates, we compared the temperature increase effect as $Q_{10}$ coefficients. In our experiment, 2.22 was the average $Q_{10}$ value, as in our previous research on soil organic matter from almost the same mountain elevation transect employing four different temperatures with only the optimal soil moisture level [5]. The sensitivity of soil respiration to temperature changes frequently has been described as the $Q_{10}$ coefficient, but cases examined in terms of moisture dependences are rather scarce. Raich and Schlesinger [30] found that soil respiration rate increased with temperature, with a $Q_{10}$ coefficient close to 2.4 for temperate regions. Lenton and Huntinford [31] reviewed a series of studies to show that most frequent $Q_{10}$ ranged between 2 and 3. The sensitivity of the soil respiration rate to temperature, as expressed by the $Q_{10}$, is not constant across the range of temperatures, given a lower $Q_{10}$ coefficient at the highest temperature (e.g. 2). In the present study the $Q_{10}$ values were also higher in the lower (5ºC-15ºC) than in the upper temperature range (15ºC-30ºC).

There are some reports that $Q_{10}$ values may depend on soil moisture [28, 32]. Also, in our study soil moisture affected the $Q_{10}$ values. The $Q_{10}$ values were the highest in dry conditions, for soil maintained at 15% WHC. It should be stressed here that $Q_{10}$ values describe relative changes in the respiration rate from one temperature to the next. Going to optimal temperature while keeping the same soil moisture parameter may enhance the respiration rate, at least for some groups of microbes that can metabolize in dry conditions. Our result differed from those obtained by [32], which found that $Q_{10}$ values increased with volumetric soil moisture. However, we applied a much wider scale of soil moisture.

Although significant decreases of soil microbial activity (respiration rate) along the elevation gradient were found in laboratory measurements, this difference of altitudes had no significant effect on $Q_{10}$ coefficients. As in our previous study, respiration rate differed between elevations, but $Q_{10}$ coefficients did not [5]. The thermal sensitivity of soil organic matter originating from slightly colder and more humid climate zones was similar to that of samples from lower (i.e. warmer and dry) part of the mountains in spite of extreme differences in soil water regime.

The $Q_{10}$ coefficients differed between organic layers, with the bottom (Ofh) layer being more temperature-sensitive than the Olf layer. These results agree with a theory of activation energy. Differences in the thermal sensitivity of different soil horizons have been reported before, but the results and conclusions in the literature are not consistent. Conen et al. [33] did not find differences between soil sensitivity to temperature for young and old soil carbon from cereal fields. It was proven that surface organic matter was more sensitive to temperature than the deeper layers of forest or grassland soils [12, 13, 34]. Furthermore, other studies showed that more decomposed organic matter may be more temperature-sensitive [8, 25]. We compared also the dependence of $Q_{10}$ on soil organic matter quality in different moisture conditions, expressing soil quality as continuous changes of C:N ratios. Those ratios depend on the decomposition stage as well as the initial properties of litter, although using C:N ratio as a measure of soil organic matter quality is to some extent a simplification. Anyway, C:N ratios have recently been suggested as indicators of carbon sequestration potential in soils [35]. Soil organic matter consists of an unusual variety of compounds with different chemical characteristics and physical availability. However, using even such a simple index of soil quality seems to be more suitable than assuming equal sensitivity of whole soil C-pool [36]. The values of C:N ratios in the examined Olf and Ohf organic layers overlapped. The relationship between $Q_{10}$ and the C:N ratios in particular moisture conditions was significant only at 75% WHC, the most optimal soil moisture for respiration rate, when $Q_{10}L$ and $Q_{10}H$ decreased with increasing C:N ratio. This indicates the important role of organic matter quality and nutrient availability for soil microorganisms [37]. Carbon substrate quality is not a sole factor influencing the temperature sensitivity of SOM. In natural systems the relationship between temperature sensitivity of decomposition and carbon availability may be obscured by complex interactions between temperature and a range of other biological factors influencing the rate of decomposition, e.g. activity of soil fauna [38]. Especially in sub-optimal moisture conditions, SOM quality may determine also other soil properties that allow appropriate use of water and access to oxygen [39].

## Conclusions

We showed that even such a short altitudinal gradient (600 m) influences soil microbial activity. While soil sensitivity to climatic factors did not differ significantly between the stands from different altitudes, at each altitude the respiration of lower organic layer Ofh was more sensitive to temperature changes than respiration of the upper Olf layer. The differences between $Q_{10}$ values suggest that climatic warming with different magnitudes of precipitation may have stronger effect on the respiration of the deeper organic layer containing a larger pool of recalcitrant carbon than the upper layers. Thus, there is a continuing need for careful, detailed investigations of the dependence of soil biological reactions to temperature and soil moisture changes. The changes not only in microbial activity but also in microbial community structure need to be studied, particularly in terms of the different fractions of soil organic matter, as soil consists of an unusual variety of compounds with different chemical characteristics and physical availability.

## Acknowledgements

We thank Ryszard Laskowski for helpful discussions and suggestions about the statistics. This work was funded by Jagiellonian University, grant No. DS/WBiNoZ/INoS/759/06.

## References

1. HOWARD D.M., HOWARD P.J.A. Relationships between $CO_2$ evolution, moisture content and temperature for a range of soil types. Soil Biol. Biochem. **25**, 1537, **1993**.
2. LIŃSKA M., MARYAŃSKI M., LASKOWSKI R. Effect of temperature on humus respiration rate and nitrogen mineralization: Implications for global climate change. Biogeochemistry **44**, 239, **1999**.
3. SCHLESINGER W.H., ANDREWS J.A. Soil respiration and the global carbon cycle. Biogeochemistry **48**, 7, **2000**.
4. BEKKU Y.S., NAKATSUBO T.N., KUME A., ADACHI M., KOIZUMI H. Effect of warming on the temperature dependence of soil respiration in arctic, temperate and tropical soil. Appl. Soil Ecol. **22**, 205, **2003**.
5. NIKLIŃSKA M., KLIMEK B. Effect of temperature on the respiration rate of forest soil organic layer along an elevation gradient in Polish Carpathians. Biol. Fertil. Soils **43**, 511, **2007**.
6. KIRSCHBAUM M.U.F. Will changes in soil organic carbon act as positive or negative feedback on global warming? Biogeochemistry **48**, 21, **2000**.
7. DAVIDSON E.A., JANASSENS I.A. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature **440**, 165, **2006**.
8. KNORR W., PRENTICE I.C., HOUSE J.I., HOLLAND E.A. Long-term sensitivity of soil carbon turnover to warming. Nature **433**, 298, **2005**.
9. FANG C., SMITH P., SMITH J.U. Is resistant soil organic matter more sensitive to temperature than the labile organic matter? Biogeosciences **3**, 65, **2006**.
10. VANHALA P., KARHU K., TUOMI M., SONNINEN E., JUNGNER H., FRITZE H., LISKI J. Old soil carbon is more temperature sensitive than the young in an agricultural field. Soil Biol. Biochem. **39**, 2967, **2007**.
11. THORNLEY J.M., CANNEL M.G.R. Soil carbon storage response to temperature: an hypothesis. Ann. Bot. **87**, 591, **2001**.
12. CHRISTENSEN T.R., JONASSON S., CALLAGHAN T.V., HAVSTRÖM M. On the potential $CO_2$ release from tundra soil in a changing climate. Appl. Soil Ecol. **11**, 127, **1999**.
13. KÄHKÖNEN A., WITTMANN C., KUROLA J., ILVESNIEMI H., SALKINOJA-SALONEN M.S. Microbial activity of boreal forest soil in a cold climate. Boreal Environ. Res. **6**, 19, **2001**.
14. RANNEKLEV S.B., BÅÅTH E. Temperature-driven adaptation of the bacterial community in peat measured by using thymidine and leucine incorporation. Appl. Environ. Microbiol. **67**, 1116, **2001**.
15. WALDROP M.P., FIRESTONE M.K. Altered utilization patterns of young and old soil C by microorganisms caused by temperature shifts and N additions. Biogeochemistry **67**, 235, **2004**.

16. BURTON A.J., PREGITZER K.S., ZOGG G.P., ZAK D.R. Drought reduces root respiration in sugar maple forest. Ecol. Appl. **8**, 771, **1998**.
17. KNOEPP J.D., SWANK W.T. Using soil temperature and moisture to predict forest soil nitrogen mineralization. Biol. Fertil. Soils **36**, 177, **2002**.
18. POWERS R.F. Nitrogen mineralization along an altitudinal gradient: interactions of soil temperature, moisture and substrate quality. For. Ecol. Manage. **30**, 19, **1990**.
19. BERG B., VIRZO de SANTO A., RUTIGLIANO F.A., FIERRO A., EKBOHM G. Limit values for plant litter decomposition in two contrasting soils-influence of litter elemental composition. Acta Oecol. **24**, 295, **2003**.
20. WARDLE D.A., NILSSON M.C., ZACKRISSON O., GALLET C. Determinants of litter mixing effect in a Swedish boreal forest. Soil Biol. Biochem. **35**, 827, **2003**.
21. POWLSON D. Why soil amplify climate change? Nature **433**, 204, **2005**.
22. GRODZIŃSKA K., SZAREK-ŁUKASZEWSKA G. Polish Mountain forest: Past, present and future. Environ. Poll. **98**, 369, **1997**.
23. FANG C., MONCRIEF J.B. The dependence of soil $CO_2$ efflux on temperature. Soil Biol. Biochem. **33**, 155, **2001**.
24. GRODZIŃSKA K., GODZIK B., FRĄCZEK W., BADEA O., OSZLANYI J., POSTELNICU D., SHPARYK Y. Vegetation of the selected forest stands and land use in the Carpathian Mountains. Environ. Poll. **130**, 17, **2004**.
25. FIERER N., SCHIMEL J.P., HOLDEN P.A. Variations in microbial community composition through two soil depth profiles. Soil Biol. Biochem. **35**, 167, **2003**.
26. AGNELLI A., ASCHER J., CORTI J., CECCHERINI M.T., NANNIPIERI P., PIETRAMALLARA G. Distribution of microbial communities in a forest soil profile investigating by microbial biomass, soil respiration and DGGE of total and extracellular DNA. Soil Biol. Biochem. **36**, 859, **2004**.
27. PIETIKÄINEN J., PETTERSSON M., BÅÅTH E. Comparison of temperature effects on soil respiration and bacterial and fungal growth rates. FEMS Mic. Ecol. **52**, 49, **2005**.
28. CONANT R.T., DALLA-BETTA P., KLOPATEK C.C., KLOPATEK J.M. Controls on soil respiration in semiarid soils. Soil Biol. Biochem. **36**, 945, **2004**.
29. WINKLER J.P., CHERRY R.S., SCHLESINGER W.H. The $Q_{10}$ relationship of microbial respiration in a temperate forest soil. Soil Biol. Biochem. **28**, 1067, **1996**.
30. RAICH J.W., SCHLESINGER W.H. The global carbon dioxide flux in soil respiration and its relationships to vegetation and climate. Tellus **44**, 81, **1992**.
31. LENTON T.M., HUNTINFORD C. Global terrestrial carbon storage and uncertainties in its temperature sensitivity examined with a simple model. Global Change Biol. **9**, 1333, **2003**.
32. QI Y., XU M., WU J. Temperature sensitivity of soil respiration and its effects on ecosystem carbon budget: nonlinearity begets surprises. Ecol. Model. **153**, 131, **2005**.
33. CONEN F., LEIFELD J., SETH B., ALEWELL C. Warming mineralizes young and old carbon equally. Biogeosciences **3**, 515, **2006**.
34. LISKI J., ILVESNIEMI H., MÄKELÄ A., WESTMAN C.J. $CO_2$ emission from soil in response to climatic warming are overestimated – the decomposition of old soil organic matter is tolerant to temperature. Ambio **28**, 171, **1999**.
35. de VRIES W., REINDS G.J., GUNDERSEN P., STERBA H. The impact of nitrogen deposition on carbon sequestration in European forests and forest soils. Global Change Biol. **12**, 1151, **2006**.
36. HARTLEY I.P., INESON P. Substrate quality and the temperature sensitivity of soil organic matter decomposition. Soil Biol. Biochem. **40**, 1567, **2008**.
37. LIU S.H., LI L.H., HAN X.G., HUANG J.H., SUN J.X., WANG H.Y. Respiratory substrate availability plays a crucial role in the response of soil respiration to environmental factors. Appl. Soil Ecol. **32**, 284, **2006**.
38. FIERER N., CRAINE J.M., McLAUCHLAN K., SCHIEMEL J.P. Litter quality and the temperature sensitivity of decomposition. Ecology **86**, 320, **2005**.
39. MILLER A.E., SCHIMEL J.P., SICKMAN J.O., MEIXNER T., DOYLE A.P., MELACK J.M. Mineralization responses at near-zero temperatures in three alpine soils. Biogeochemistry **84**, 233, **2007**.